

Zonation and Evolution of a Rocky Bottom Hydroid Community*

FERDINANDO BOERO¹ & EUGENIO FRESI²

¹ Istituto di Zoologia dell'Università di Genova, Via Balbi 5, I-16126 Genova, Italy.

² Stazione Zoologica di Napoli, Laboratorio di Ecologia del Benthos, Punta S. Pietro 1, I-80077 Ischia Porto (Napoli), Italy.

With 10 figures

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Abstract. The distribution in space and time of a hydroid community on a vertical rocky substratum is studied from the surface to 20 m depth. The role of the major environmental factors (light, water movement, temperature) in determining the zonation is evaluated. The results are compared with the main zonation models of Mediterranean benthos. The autecology of the collected species is briefly described.

Problem

In their polypoid form, hydroids are among the most abundant and characteristic sessile animals of marine hard-bottom communities. Their species richness, morphologic plasticity, and ecological specialization have led various authors (*e.g.* RIEDL, 1959; MERGNER, 1977) to use the group as an indicator of different overall environmental conditions.

Notwithstanding this, general knowledge on the ecology of hydroids is rather incomplete and scattered in the literature (see BOERO, 1984, for a review). Regarding the Mediterranean Sea, the ecology of the group has been studied by RIEDL (1959) in marine caves, by PICARD in coralligenous formations (1951a) and on *Posidonia oceanica* (L.) DELILE beds (1952), by BOERO in the mussel belt (1981a) and on *P. oceanica* beds (1981b), and by FRESI *et al.* (1982) and BOERO *et al.* (1985) again in *Posidonia* meadows. The ecology of single taxa is investigated in works such as SVOBODA'S (1979) on *Aglaophenia* and BOUILLON'S (1975) on *Paracoryne huvei* PICARD. Further information is found in taxonomic works, the most important of which is that of BRINCKMANN-VOSS (1970) on *Athecata-Capitata*. NEPPI (1917) reported on hydroids of the Gulf of Naples and included

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data on their seasonality. STECHOW (1919, 1923) reported on species found in Portofino, as did ROSSI (1949–50; 1961).

The present investigation was carried out in the framework of a research project dealing with the vertical zonation of hard-bottom benthic communities in relation to gradients of major environmental factors such as light and water movement (SARA *et al.*, 1978). The aim of our work was to identify the zonation pattern of hydroids relative to that of the community as a whole and to identify the responsible ecological parameters. Further points of interest were the variability in time of this distribution and the consistency of population units, as well as the variability of single species abundances and reproductive activity.

Material and Methods

Samples were collected in November 1976 along a transect on a cliff of the Portofino Promontory. A general description of the sampling site is available in SARA *et al.* (1978). The rocky wall is almost vertical to a depth of 10 m and then begins to slope with a number of large steps. All samples were taken on vertical portions of the cliff; the geographic orientation of all samples was the same. Standard surfaces of 20 x 20 cm were scraped; all organisms were collected and immediately preserved.

In the first 2 m depth, starting from the "biologic zero" (BOUDOURESQUE & CINELLI, 1977), samples were taken at 0.5 m intervals, and at 1 m intervals thereafter down to 20 m, for a total of 23 collections. Hydroid abundances were estimated by counting the absolute number of polyps of each species.

A second sampling procedure involved subdividing the transect into five zones (0–0.5; 0.5–5; 5–10; 10–15; 15–20 m).

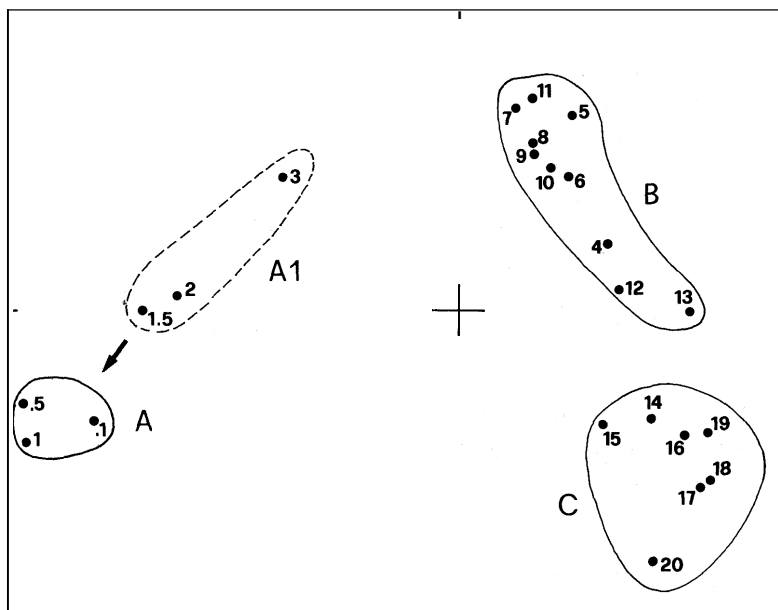


Fig. 1. Ordination model (Q-mode) of the 23 samples obtained on standard surfaces, where $x = \log(x+1)$, in the plane defined by the two first principal components. Each number identifies a depth. Both components are significant. Variances explained: PC1 = 31.93%; PC2 = 12.12%.

Monthly collections were carried out throughout 1980 in a 2m wide band within each zone. In this series the collection of hydroids was visually oriented, the abundances estimated *in situ*. Each species was given a value from 1 to 3, that is: 1 = scarce; 2 = moderately abundant; 3 = abundant.

Further samples were taken along the promotory coast in order to obtain more complete faunistic data, although these data were not included in the present analysis.

Regarding environmental parameters, light was measured by means of an underwater photometer, water movement was estimated by the method of plaster balls as proposed by Muus (1968), and temperature values were obtained from DELLA CROCE *et al.* (1979, 1980), who monitored hydrological parameters in the area.

Data analysis. Numerical data, both for species and physical parameters, were analyzed by autovectorial methods. Two different techniques were used: Principal Components Analysis (PCA) both in R- and Q-mode (ORLOCI, 1975) and RQ-Factorial Analysis (HATHEWAY, 1971), also known under the designation Reciprocal Averaging (HILL, 1973). The latter was also used for a simultaneous analysis of biotic and abiotic variables. For this purpose the variables were rendered homogeneous by boolean data coding, describing for each variable three "states" or modalities: low, mean, high. The original variable vectors were therefore transformed into three new vectors, each describing one of the three modalities.

The results of these analyses were tested for significance utilizing the method proposed by FRONTIER (1974).

A cluster analysis, performed according to JANCEY (1974), was used for the automatic construction of clusters in the individual ordination models.

Results

1. Hydroid zonation along the transect

The first series of samples (standard surfaces) yielded 60 taxa, 56 of which are identified to the species level. The representatives of the genus *Eudendrium* were in such poor condition that their identification to the species level was not possible; they were therefore not considered in the following analysis, despite their quantitative importance. Of the remaining 59 taxa, a set of 45 whose frequency was higher than 10% was selected. These underwent a PCA (Q-mode) (Fig. 1). In the resulting model, points are arranged along a parabola in which three groups are formed by clustering the sample-points: group A, towards the negative pole of PC1 to which the sub-group A1 can be attributed; group B, situated in the positive space of PC1 as is group C, the two being opposed along PC2.

Cluster A consists of the first three stations (0.1, 0.5, 1 m) and is slightly separated from sub-group A1, comprising stations down to 3 m depth. Cluster B, separated from this complex by a sharp discontinuity, includes stations from 4 to 13 m. Cluster C consists of the remaining stations of the transect.

In order to obtain species groups characterizing the three depth-zones from this model, an RQA was performed. This technique allows the contemporary projection of species-points and variable-points onto the same factorial space, where proximities reflect actual affinities, whose measure is given by a canonical correlation coefficient (ORLOCI, 1975). In this case correlations between species and sample-points are fairly good both in the space of F1 and F2. Fig. 2 shows the resulting ordination model in the plane of the first two factors. Station-points are arranged in a similar, although specular pattern to that obtained by PCA (Fig. 1). Differences consist in that group B and C of the PCA model are

compacted in a single linear cluster. Samples from 1.5 to 3 m maintain their intermediate position.

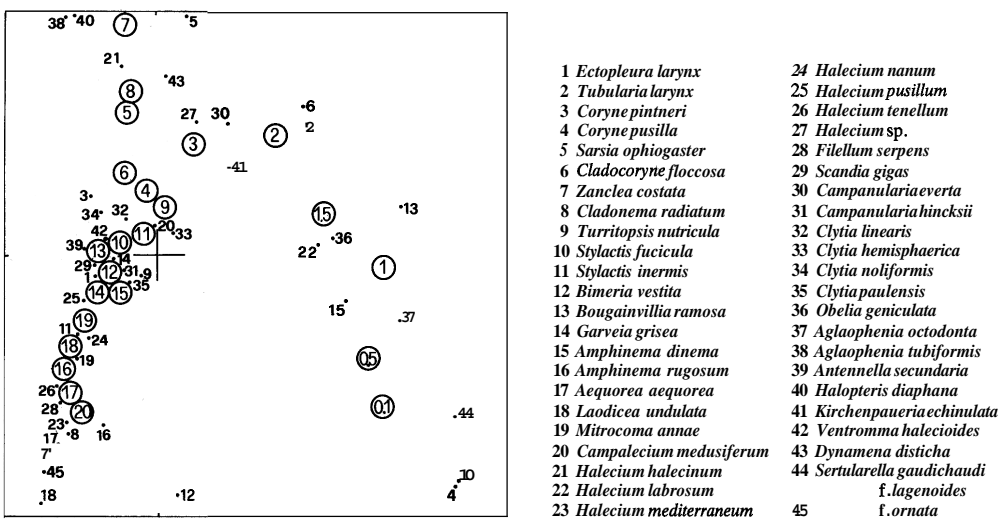


Fig. 2. Ordination model in the plane defined by the first two factors of species and samples on standard surfaces (abundances coded), obtained by RQ analysis. Sample depth in circles. Each species position is indicated by a point with the relative number. Both factors are significant. Variances explained: F1 = 23.74%; F2 = 12.54%. The correlation coefficient between stations and species is 0.56 for the first factor and 0.45 for the second.

The species which characterize the superficial stations are: *Coryne pusilla*, *Stylactis fucicola*, *Bougainvillia ramosa*, *Amphinema dinema*, *Halecium labrosum*, *Obelia geniculata*, *Sertularella gaudichaudi* f. *lagenoides*, *Aglaophenia octodonta*.

Ectopleura larynx, *Coryne pintneri*, *Zanclaea costata*, *Cladonema radiatum*, *Turritopsis nutricula*, *Stylactis inermis*, *Bimeria vestita*, *Garveia grisea*, *Amphinema rugosum*, *Aequorea aequorea*, *Laodicea undulata*, *Mitrocorna annae*, *Filellum serpens*, *Scandia gigas*, *Campalecium medusifera*, *Halecium mediterraneum*, *H. nanum*, *H. pusillum*, *H. tenellum*, *Campanularia hincksii*, *Clytia hemisphaerica*, *C. linearis*, *C. noliformis*, *C. paulensis*, *Antennella secundaria*, *Ventromma halecioides*, and *Sertularella gaudichaudi* f. *ornata* are related to deep stations.

A third group, consisting of *Tubularia larynx*, *Sarsia ophiogaster*, *Cladocoryne floccosa*, *Halecium halecinum*, *Campanularia everta*, *Aglaophenia tubiformis*, *Halopteris diaphana*, *Kirchenpaueria echinulata*, and *Dynamena disticha*, show preference for the transition zone.

A common trend of both PCA and RQA models is the sharp species change occurring below 3 m. This produces the above-mentioned parabolic distortion, that could mask significant patterns, especially in the distal portion of the transect. By performing an RQA on all samples except the first six (0.1–3 m) the distortion can be removed.

Results of this analysis are shown in Fig.3. Station-points are now linearly arranged along F1, confirming the essentially continuous grading of the population from 4 to 20m.

The values of the environmental factors decrease exponentially along the transect (Fig.4) and are highly correlated with one another. Fig. 5 shows the

Fig. 3. Ordination model obtained by RQ analysis performed on all samples except the first six (0.1-3m) in the plane defined by the first two factors. Stations are individuated by their depths. Only F1 is significant. Variance explained: F1= 19.73%; F2 = 12.97%.

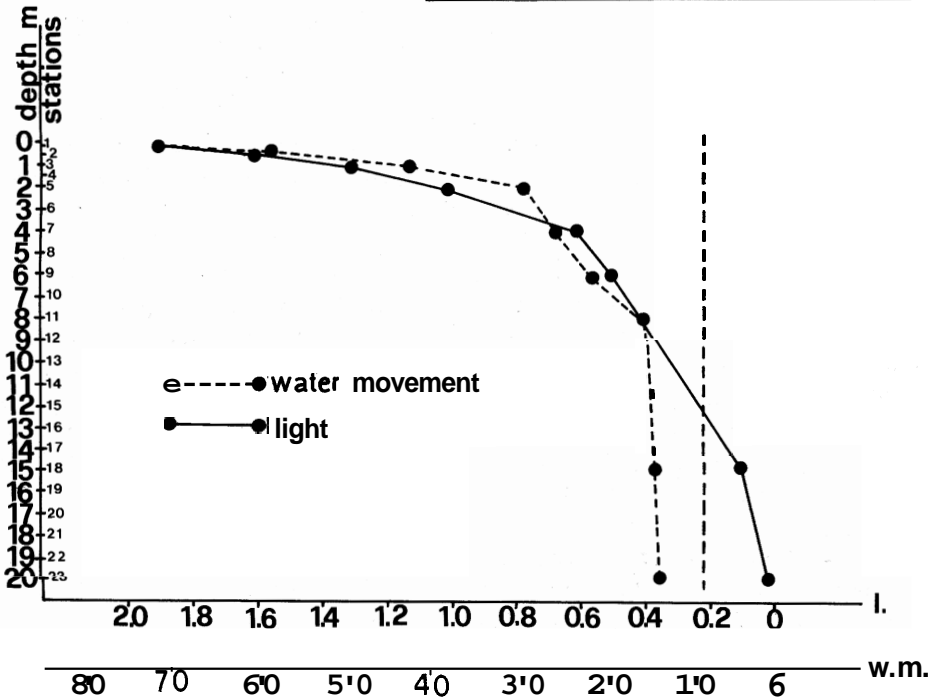
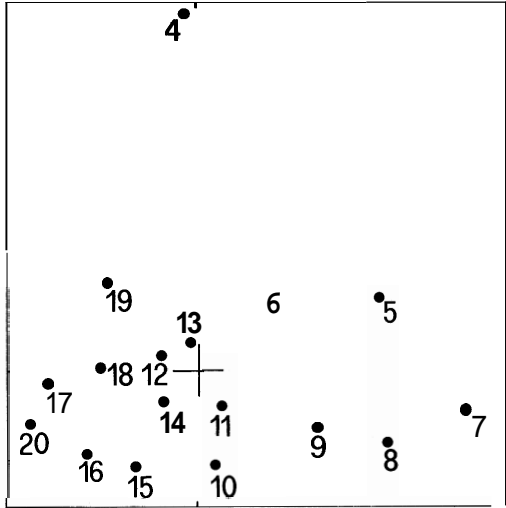


Fig. 4. Extinction curves of the factors light ($mW \cdot cm^{-2}$) and water movement along the Portofino Promontory. Water movement is expressed as percent consumption of plaster balls immersed for 24h (the dashed line indicates consumption in still water).

combined variation of light and water movement obtained by a PCA (R-mode). The amplitude of the variation reaches its maximum in the first two meters, corresponding to the exponential portion of the extinction curves. The first axis of this ordination was tested for correlation with the first factor of the RQ ordination model of hydroids (Fig. 2). The results show that the two variables are highly and significantly correlated ($r = -.887$; $p < 0.1$) demonstrating a remarkable dependence of the faunal distribution on the combined variation of light and water movement.

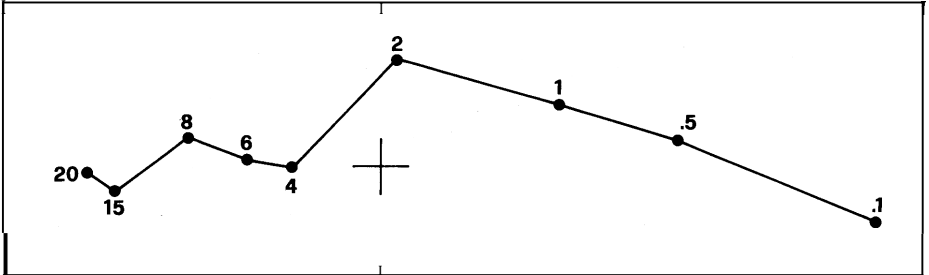


Fig.5. Ordination model of the stations at which light and water movement were measured (PC analysis - R mode) in the plane defined by the two first principal components. PC2 is not significant. Variance explained: PC1 = 98.38%.

This analysis, however, does not permit the discrimination of the influence of each physical factor *per se*. To overcome this problem a simultaneous analysis of both the biotic and abiotic variables was performed by means of an RQA (Fig. 6).

The variance extracted by the first two factors is rather low. This is often the case when autovectorial analysis deals with boolean data and does not affect the results (CÉHSSAT, 1976; CINELLI *et al.*, 1976).

The general pattern of this model resembles that of the preceding ones: stations are scattered along a parabola whose right portion includes the most superficial ones. Again, the most relevant discontinuities are found in the upper part of the transect whilst, beginning at 4 m, stations are ordered in an almost continuous cloud.

When physical factors and their "states" are plotted onto this model, high and medium values correspond to the right and the apical parts of the parabola. Low values correspond to the left tail of the curve. There are no major differences in the distribution of these two variables as their equivalent modalities are plotted rather close to one another. Nevertheless, high water movement values are more strongly correlated with the uppermost stations (0.1–1.5 m) than high light values.

2. Time series

The above results give a static picture of the hydroid zonation along the transect. The question which arises is whether this distribution pattern is

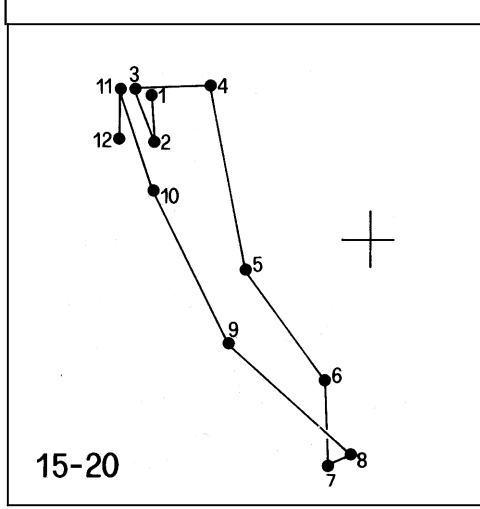
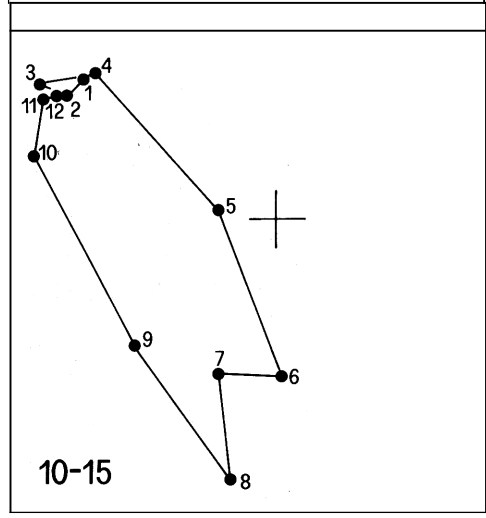
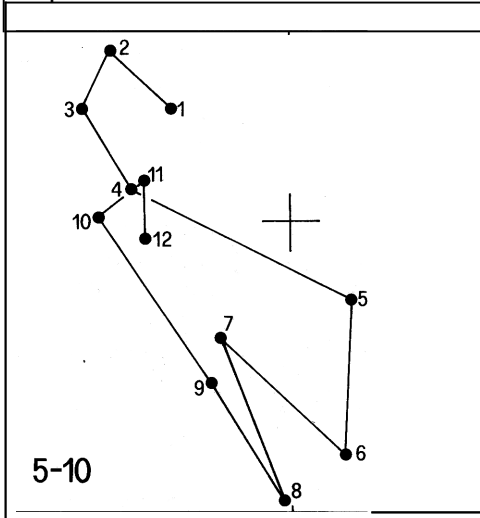
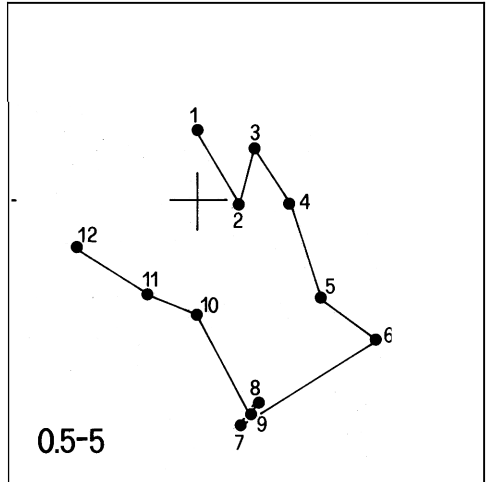
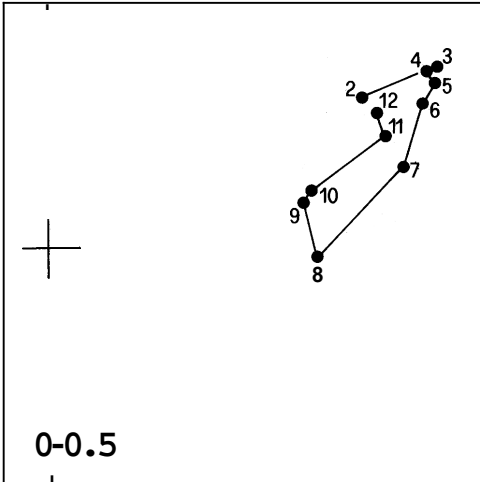


Fig.7. Evolution of the hydroid population in a time series: PC analysis in the plane of the first two principal components. All diagrams are in the same plane and have been split for ease of reading. Sampling depths are indicated in the lower left-hand corner; numbers indicate months. Both components are significant. Variance explained: PC1 = 24.98%; PC2 = 11.42%.

pattern is almost identical to the models obtained through the preceding synchronic analysis.

The individual plots clearly describe the seasonal changes of the population at the various levels. All show a common trend along the second ordination axis, *i. e.* the observations from October to April are consistently located near the negative pole. In general, the time trajectories are almost parallel to this axis and show a more or less closed shape.

The uppermost level (0–0.5 m) shows a compact cycle without major seasonal drifts. The second level (0.5–5 m) has the most pronounced drift along the first axis, again pointing to its intermediate character. From here on, time trajectories lengthen along the second axis emphasizing the separation of the two “seasonal poles”.

The study of the time series led to the identification of the species characterizing the three levels:

1. Superficial level (0–0.5 m)

- a. species present throughout the year: *Coryne muscoides*, *Coryne pusilla*, *Stylactis fucicula*, *Hebella parasitica*, *Campanularia integra*, *Obelia geniculata*, *Aglaophenia octodonta*, *Sertularella gaudichaudi* f. *lagenoides*.
- b. species present in the warm season: none
- c. species present in the cold season: *Sarsia ophiogaster*.

2. Intermediate level (0.5–5 m)

- a. species present throughout the year: *Cladocoryne floccosa*, *Eudendrium capillare*, *Halecium mediterraneum*, *Filellum serpens*, *Scandia gigas*, *Campanularia hincksii*, *Obelia geniculata*, *Aglaophenia kirchenpaueri*, *A. octodonta*.
- b. species present in the warm season: *Eudendrium racemosum*, *Dynamena disticha*.
- c. species present in the cold season: *Tubularia larynx*, *Sarsia ophiogaster*.

3. Deep level (5–20 m)

- a. species present throughout the year: *Eudendrium ramosum*, *Halecium mediterraneum*, *Filellum serpens*, *Scandia gigas*, *Campanularia hincksii*, *Aglaophenia elongata*, *Antennella secundaria*.
- b. species present in the warm season: *Eudendrium racemosum*, *Clytia linearis*, *Dynamena disticha*.
- c. species present in the cold season: *Stylactis inermis*, *Bimeria vestita*, *Gaweia grisea*, *Amphinema rugosum*, *Eudendrium fragile*, *E. glomeratum*, *Obelia dichotoma*, *Sertularella crassicaulis*.

Other species, such as *Clytia hemisphaerica* and *Halecium pusillum*, are very frequent and often abundant at almost every depth.

Seasonal fluctuations of the population were tested for correlation with the variation in the temperature. This parameter is thought to be the main ecological factor for hydroid life cycles. As DELLA CROCE *et al.* (1979; 1980) measured this parameter at only three levels that are applicable to this analysis (0, 10, 25 m) we compacted our levels accordingly: level A (0–0.5 m); level B (10–15 m); level C (15–20 m). The summer thermic stratification, with a first thermocline within level B, justified this division.

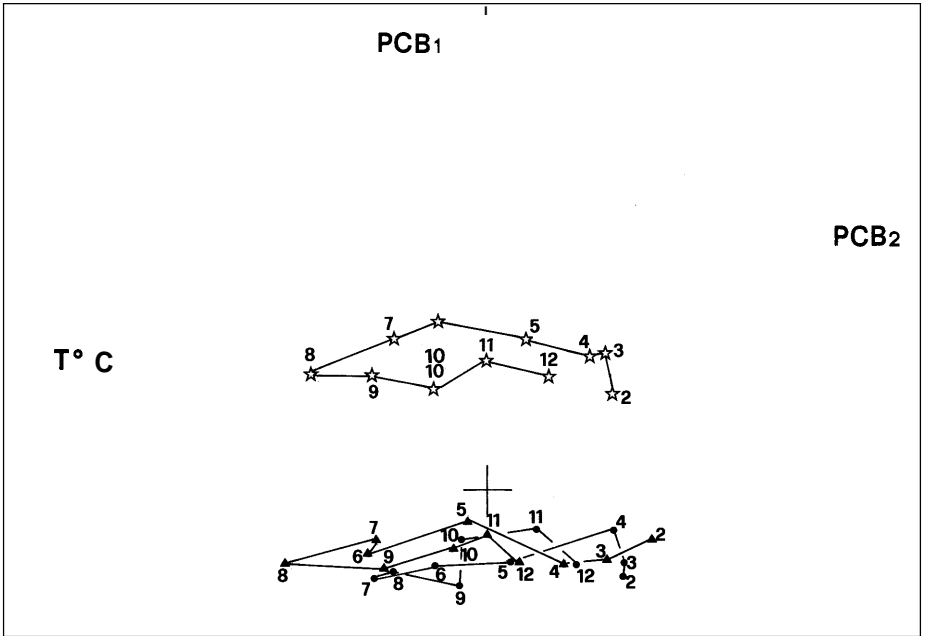


Fig. 8. Variation of the two first principal components of the biological time series analysis (PCB1, PCB2) and temperature ($T^{\circ}\text{C}$), obtained with PC analysis (R-mode) on the plane of the two first principal components. Numbers indicate months. Symbols indicate depths: stars = 0–0.5; triangles = 10–15; dots = 15–20m. Variables' coordinates are derived according to $x = B_{i1}\sqrt{\lambda_1}$; $y = B_{i2}\sqrt{\lambda_2}$ where b = eigenvector, λ = eigenvalue. Variance explained: PC1 = 46.28%; PC2 = 40.56%.

The PCA (R-mode) included the two first PC of the time series ordination and temperature. The resulting model is shown in Fig. 8. Points are so arranged along the first axis as the winter-spring observations lay in the positive space and those from summer in the negative space. The second axis clearly separates level A from the others. The “loading” of the variables in the first axis is high for temperature and PCB2, low for PCB1. In the second axis temperature has a low “loading”, whereas PCB1 has a high “loading” and PCB2 a moderate one.

3. Fertility periods

The evolution in time of fertility was studied for 29 species. This was done not only to identify the reproductive periods of the individual species, but also to correlate this physiological parameter of the population to the observed zonation. The data were analyzed by means of an RQA performed on a boolean matrix where the presence of gonophores is coded as 1 and their absence as 0. The resulting ordination model, shown in Fig. 9 (stations) and Fig. 10 (species), has again been split for ease of reading.

The observations are scattered along the first ordination axis in an almost linear manner. With the exception of the first level, most have a central

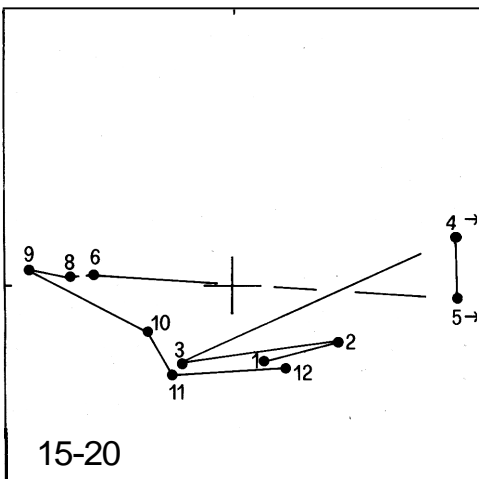
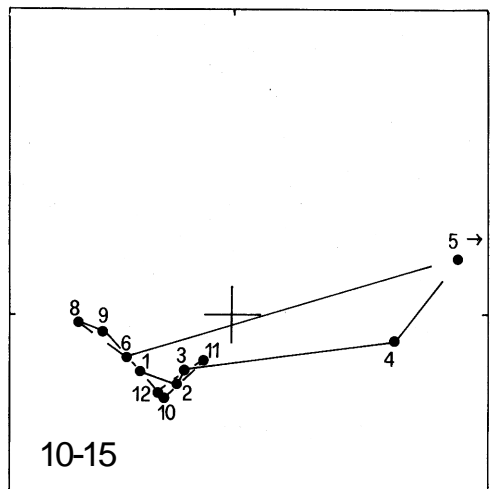
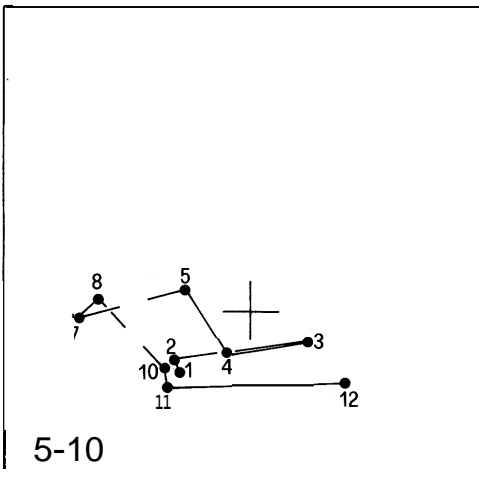
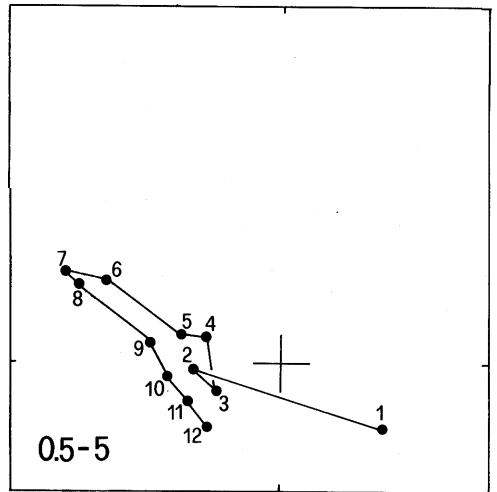
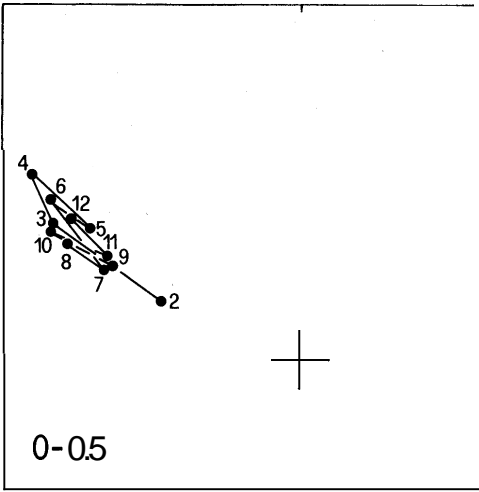


Fig.9. Evolution of the fertility periods of 29 species along the time series analyzed in Fig. 7. RQ analysis ordination model in the plane of the first two factors. All diagrams are in the same plane and have been split for ease of reading. Sampling depths are indicated in the lower left-hand corner; numbers indicate months. Variance explained: F1 = 13.47%; F2 = 11.35%. The correlation coefficient between stations and species is 0.92 for F1 and 0.84 for F2.

ordination, although there is a tendency for summer observations to be located towards the left part of the graph. At the two deeper levels the April and May observations are strongly set off towards the positive pole.

The second axis places the upper level opposite the remaining ones, with the second level in the usual intermediate position.

The ordination of species shows three separate clusters (Fig. 10). The first includes four species which are fertile in the warm season: they are superficial or intermediate. The second cluster is formed by seven species, fertile between winter and summer: they are mainly superficial and intermediate. The most numerous cluster is that containing the species fertile in winter: the majority have a deep location.

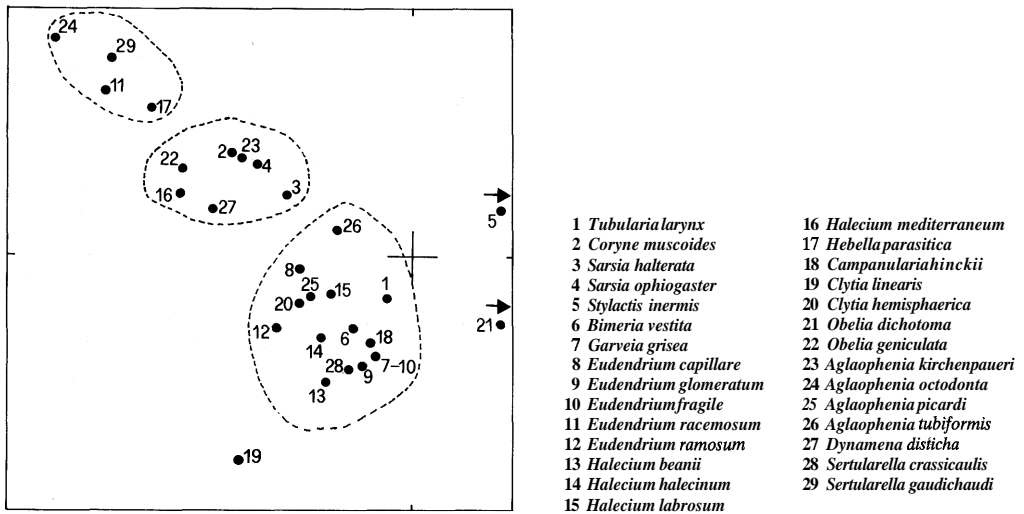


Fig. 10. Ordination model in the plane defined by the first two factors of the 29 species whose fertility periods have been analyzed in Fig. 9. Variance explained and correlation coefficients as in Fig. 9.

Discussion

1. The transect

The ordination models consistently show the same general pattern: the stations are arranged along the first axis from superficial to deep, describing a clear depth-related zonation. This zonation is characterized by a marked discontinuity separating the population inhabiting the first 3 m from that of the lower levels. These latter stations are arranged in an elongate cluster without relevant discontinuities.

Such a configuration suggests the existence of two widely separate community units; the transition between them occurs in a narrow band between 1.5 and 3 m. Although very clear, this pattern has a non-linear character. While the first axis

orders the observations along the depth gradient, the second induces a parabolic curvature. This type of distortion is mainly due to strong “disjunction” of the superficial samples from the remaining ones, paralleled by high species change occurring in the transition zone. In fact, the removal of the stations above the discontinuity reveals a linear and continuous depth-related variation in the deep cluster.

Models of this type reflect a non-linear response to environmental factors changing in relation to depth. The discontinuity marks the cenotic space where the influence of these factors is no longer felt in an exponential manner. From there on the response becomes linear and the cenocline has no major discontinuities.

Considering the variation with depth of the two measured factors, light and water movement intensity, it is obvious that the exponential phase of their extinction curves coincides with the cenotic discontinuity. This becomes more evident when these variables are analyzed simultaneously with the biological ones: the superficial community appears to be differentiated by high and medium levels of environmental energy.

The high correlation between the two factors renders the discrimination of their individual action on the community difficult. Our model, however, points to a greater influence of water movement in the uppermost part of the transect. This is not surprising as tolerance to mechanical stresses may be much more important in this zone than tolerance to high illumination levels. Morphological adaptations exhibited by several species such as *Plumularia obliqua*, *Ventromma halecioides*, and *Halecium pusillum* (BOERO, 1981 a, b) point to this interpretation.

2. Time series

The analysis of the diachronic series reveals a major fact: the pattern of the zonation persists in time, preserving the characteristics described for the transect. The two communities, between which the transition zone is still evident (0.5–5 m), remain separated year round.

The time drifts are almost parallel to the second axis that, therefore, incorporates information on seasonal succession as well as on the erratic fluctuations of the communities. The negative pole of this axis represents the “warm” season, while the positive pole represents the “cold” season. The transition between the two clusters is rather abrupt in most cases.

The amplitude of the drifts each level undergoes throughout the year tends to increase with increasing depth: while that of the superficial community is rather compact, those of the remaining levels are relatively elongated. Such a configuration suggests that minor seasonal changes occur in the superficial community, which exhibits a remarkable stability in time despite its low diversity. This lack of seasonal succession is due to the large group of species found throughout the year. The intermediate zone (0.5–5 m) shows a time trajectory that partly parallels the first axis and therefore shows “deep” or “superficial” resemblances according to the season. This stresses its character of ecological transition. The time drifts in the following levels are surprisingly high. One would have

expected smaller seasonal changes at depths where the physical variability is likely to be much lower than near the surface.

As mentioned above, temperature is thought to be one of the most important time-varying ecological factors for hydroids. When temperature is correlated to the ordination axes of the time series (Fig. 8) it is evident that, while it has practically no effect on the zonal factor of the population (PCB1), it is correlated with the seasonal factor (PCB2). The value of this correlation ($r_{\text{PCB2}, T^{\circ}\text{C}} = -0.383$), however, is not as relevant as might be expected considering the different thermic variability in the different levels of the water column.

This implies that the seasonal succession is only in part correlated to temperature changes. In fact the surface community, although submitted to relevant and frequent temperature changes (mean yearly $\Delta T = 8.94^{\circ}\text{C}$), undergoes limited modifications throughout the year. The deep community, on the other hand, notwithstanding its more stable thermic condition (mean yearly $\Delta T = 6.18^{\circ}\text{C}$) shows conspicuous seasonal drifts.

As temperature plays only a minor role (at least directly) in determining successions, another explanation must be sought. The competition for substratum is certainly involved at least as far as the deep community is concerned. The macroalgae, for example, have been observed to outcompete a considerable number of cold season hydroids, especially certain large *Eudendrium* (*E. glomeratum*, *E. ramosum*) and their associated species (*E. fragile*, *Gaweia grisea*, *Bougainvillia ramosa* etc.) at the onset of the warm season. The winter hydroids, therefore, disappear between April and May and resettle starting in October.

The imperfect correlation between temperature and population composition can be also explained by the discovery of circannual rhythms in hydroids (BROCK, 1975). It has been shown that *Laomedea flexuosa* can modify its environmental strategies before environmental (mainly temperature) changes actually occur. This could lead to a lack of correspondence between the observed T values and the structural changes of the hydroid population.

3. Fertility

The major result from the analysis of the fertility periods is almost continuous reproductive activity of the superficial community. This functional aspect of the population confirms the individuality of this community with respect to the intermediate and deep ones. It can be interpreted as the necessity for a continuous supply of larvae to cope with the high physical stress characterizing the superficial zone (e.g. mechanical removal of colonies from their substratum or of the substratum itself). This also explains the stability in time of this community from the structural standpoint. The relative increase in fertility observed in the superficial community during summer could be related not only to thermic conditions but also to the decrease in water movement, which may ensure a greater success of larval settlement.

The strong seasonality observed for the deeper levels reflects the variation in time of the species composition. As already mentioned, this seasonality can be due to both physical and biological phenomena affecting the intermediate and the deep community.

4. Conclusions

The vertical zonation of the hydroid syntaxon is caused by a complex gradient extending from the surface to deeper water. The exponential nature of the two main factors of this gradient (light and water movement) produces an exponential response of the community which is particularly evident in the superficial levels.

This type of response is marked by a very strong cenocline indicating a large turnover in species composition and structure of the community; this implies both morphological and functional adaptations. The cenocline observed for hydroids seems to apply to other taxa and, as suggested by **FRESI & CINELLI** (1982), to be independent of locality, substratum, and time. These authors have proposed to define it as a “superficial discontinuity” separating two main vertical domains in the neritic environment: the superficial one, characterized by high energy levels and mainly physically controlled, and a lower one, where biological interactions play a major role, in the absence (at least within limits which are still to be defined) of strong environmental gradients. According to our results these two domains exist and remain consistently separate in time.

The lower limit of the superficial community seems to coincide with the “first critical depth” defined by **RIEDL** (1964, 1971) as the boundary between the surf zone and the zone with a predominantly oscillating water body. This boundary was originally identified by **RIEDL** through the changes in orientation of planar passive filter feeders (especially *Cnidaria*). Our results show that the superficial discontinuity can also be distinguished when all growth forms of hydroids are considered; this reinforces the validity of the phenomenon. It must be stressed, however, that it is not only the quality but mainly the intensity of the mechanical energy that defines this limit. This is indicated by the form of the curve representing the quantitative variation of water movement with depth.

Beyond the superficial discontinuity the ecocline shows only linear variations even though our transect crosses **RIEDL**'s second critical depth (the boundary between oscillating and unidimensional water flows). Our deepest samples were taken below the zone in which *Eunicella cavolinii* changes its orientation, which is thought to be the best marker for this boundary.

The lack of response of the overall syntaxon to this boundary suggests that, although the second critical depth marks a change in the quality of water movement, it does not mark a corresponding change in the community structure. Again, the quantitative aspect of mechanical energy (which shows no significant change through this boundary) plays a major role with regard to the qualitative one.

Thus our results suggest the existence of at least two distinct faunal zones within the investigated depth range. We find it difficult to fit these zones within the zonation model proposed by **PÉRÈS & PICARD** (1964) and so widely used by Mediterranean benthologists. In particular, this model considers the substantial unity of the hard-bottom infralittoral community (the “biocoenose à algues photophiles”) extending from “a few centimeters below the mean sea level up to about 40m in some cases”. On soft bottoms this community coincides with that of *Posidonia oceanica* beds. It has been already demonstrated (**BOERO**, 1981a; **BOERO et al.**, 1985) that the epiphytic hydroids on *Posidonia* show a marked zonation with a sharp “superficial discontinuity”.

The existence of such a feature on both types of substrata indicates that the "étage infralittoral" is not as homogeneous as it is claimed to be. Furthermore the model of PÉRÈS & PICARD implies that the infralittoral zone is defined by critical values of light intensity and quality. This is due to the fact that these authors emphasize the vegetal component of the community as an indicator of ecological conditions.

From our results it is clear that, above the superficial discontinuity, hydrodynamic forces are probably more important than light intensity. The direct influence of the latter beyond the superficial discontinuity is difficult to assess because its extinction curve almost perfectly overlaps that of water movement and because little is known about light-induced ecological adaptations in hydroids (BOERO, 1984). This difficulty is also evident in a recent work of MARINOPULOS (1983).

The above discrepancies are due, in our opinion, to the fact that both RIEDL (1964) and PÉRÈS & PICARD (1964) give causal explanations for their zonation models that are, in a sense, monofactorial. It is obvious that this is seldom the case when ecological events are being dealt with.

Appendix

Ecology of the hydroid species of Portofino

The 90 species listed below have been found on the vertical wall along the transect where standard surfaces were sampled and the seasonal samplings carried out, or in immediately adjacent stations. The depth range is from the surface to 20 m. The basic ecological information for every species in the studied area is given.

1) *Ectopleura larynx* (WRIGHT)

Depth-range: 0.5–15 m

Occurrence: June–December, occasionally present in other months; always scarce, with small colonies of not more than four polyps.

Substratum: concretions, algae, *Eudendrium* spp., barnacles.

Reproductive period: June.

Remarks: MOORE (1939) has shown that this species sheds its hydranth at high temperature and this explains its absence in summer.

Tubularia larynx is a typical Atlantic species; it becomes abundant at Portofino when temperature conditions are similar to those of the Atlantic. *Tubularia larynx* forms a seasonal facies in the intermediate zone.

2) *Tubularia larynx* ELLIS & SOLANDER

Depth-range: 0.5–6 m

Occurrence: September–May; very abundant from November to April, scarce in May, September, October.

Substratum: concretions, algae, sponges, hydroids, barnacles, etc.

Reproductive period: November–May.

3) *Coryne muscoides* (L.)

Depth-range: 0–1 m

Occurrence: always present; frequent but never abundant.

Substratum: algae, barnacles.

Reproductive period: February, July, September.

Remarks: together with *Coryne pusilla*, to which it is very similar, *C. muscoides* is one of the typical hydroids of the first meter of depth.

4) *Coryne pintreri* SCHNEIDER

Depth-range: 5–10 m

Occurrence: November; scarce.

Remarks: found only in the samples from standard surfaces. In other localities it is relatively frequent on the leaves of *Posidonia oceanica*.**5) *Coryne pusilla* GAERTNER**

Depth-range: 0–1 m

Occurrence: always present; frequent, but never abundant.

Substratum: algae, hydroids, barnacles.

Reproductive period: March and August.

6) *Sarsia halterata* (FORBES)

Depth-range: 0.5–5 m, occasionally to 20 m.

Occurrence: January to June; frequent, never abundant.

Substratum: always embedded in sponges such as *Petrosia dura*, *Spirastrella cunctatrix*, *Chondrilla nucula*.

Reproductive period: April, May, June.

7) *Sarsia ophiogaster* (HAECKEL)

Depth-range: 0–2 m

Occurrence: October–May; frequent, occasionally abundant.

Substratum: algae, bryozoans, barnacles, muscels.

Reproductive period: February–March.

8) *Cladocoryne floccosa* ROTCH

Depth-range: 0.5–6 m

Occurrence: always present; frequent, never abundant.

Substratum: algae, bryozoans, barnacles.

Reproductive period: July.

9) *Zanclaea costata* GEGENBAUR

Depth-range: 0.5–20 m

Occurrence: always present; frequent, never abundant.

Substratum: algae, *Eudendrium*, bryozoans, *Lithophaga* (*Mollusca*).

Reproductive period: August.

10) *Cladonema radiatum* DUJARDIN

Depth-range: 10 m

Occurrence: November; rare.

Substratum: algae.

Remarks: very common in all tanks used for rearing hydroids during the present research. At 20°C it is always fertile. In the field it has been found only in the samples from standard surfaces.

11) *Thecocodium brienii* BOUILLON

Depth-range: 19 m

Occurrence: November; rare.

Substratum: concretions and algae.

Reproductive period: November.

Remarks: found only in the samples from standard surfaces.

12) *Rhysia autumnalis* BRINCKMANN

Depth-range: 7 m

Occurrence: October; rare.

Substratum: algae.

Reproductive period: October.

Remarks: this is the first record of the species outside the Gulf of Naples.

13) *Perarella schneideri* (JICKELI)

Depth-range: 5–20 m

Occurrence: always present; very frequent only on a single bryozoan species.

Substratum: *Schizoporella longirostris* (*Bryozoa*).**14) *Clava multicornis* FORSKÅL**

Depth-range: 0–0.5 m

Occurrence: November; rare.

Substratum: algae and bryozoans.

15) *Cordylophora neapolitana* (WEISSMANN)

Depth-range: 15–20 m

Occurrence: May, November, December; not frequent, locally abundant.

Substratum: algae, *Eudendrium* spp.

**16) *Cordylophora pusilla*
MOTZ-KOSSOWSKA**

Depth-range: 5 m
 Occurrence: October; frequent, locally abundant.
 Substratum: leaves of *Posidoni* *oceanicu*, the common Mediterranean seagrass.
 Reproductive period: October.
 Remarks: found a short distance from the examined wall in a sporadically studied *Posidoni* meadow (BOERO, 1981b). Occurrence and fertility period are probably wider.

17) *Turritopsis nutricula* MCCRADY

Depth-range: 0.5–5 m, occasionally to 20 m.
 Occurrence: July–November; not very frequent, never abundant.
 Substratum: algae, barnacles.
 Reproductive period: July–August.

18) *Stylactis fucicula* M. SARS

Depth-range: 0–0.5 m
 Occurrence: always present; frequent, never abundant.
 Substratum: algae, hydroids, barnacles.
 Reproductive period: April, August.
 Remarks: very small species living among the algae, growing on barnacles. It is typical of the superficial zone.

19) *Stylactis inermis* ALLMAN

Depth-range: 5–20 m
 Occurrence: October–May; very abundant from March to May.
 Substratum: algae, sponges, hydroids, barnacles, *etc.*
 Reproductive period: April–May.
 Remarks: in the three months of its maximum abundance it can cover almost everything, forming a temporary facies.

20) *Stylactis aculeata* WAGNER

Depth-range: 0.5–20 m
 Occurrence: August, November; rare.
 Substratum: gastropod shells inhabited by hermit crabs.
 Reproductive period: August, November.
 Remarks: probably more abundant and frequent; the association with hermit crabs makes its collection difficult with the methods used. It produces medusoids which live only a few hours.

21) *Bimeria vestita* WRIGHT

Depth-range: 1–20 m
 Occurrence: October–May; very frequent and occasionally abundant on *Eudendrium glomeratum* and *E. ramosum* between 10 and 20 m.
 Substratum: algae, sponges, hydroids, serpulids, bryozoans.
 Reproductive period: October–February.
 Remarks: despite of the vast array of substrata on which it can settle, *Bimeria vestita* prefers the large *Eudendrium* species; its life-cycle is similar to that of its hosts.

**22) *Bougainvillia ramosa*
(VAN BENEDEEN)**

Depth-range: 0–20 m
 Occurrence: always present; frequent, abundant only in May.
 Substratum: algae, hydroids, mussels, polychaete tubes, barnacles.
 Reproductive period: May.
 Remarks: the morphological variation of this species is well known. In the present study almost only small colonies were found. Larger colonies have been found below 30 m.

23) *Garveia grisea* (MOTZ-KOSSOWSKA)

Depth-range: 5–20 m
 Occurrence: October–May; frequent, occasionally abundant.
 Substratum: algae, hydroids, bryozoans.
 Reproductive period: October–January.
 Remarks: together with *Bimeria vestita* it prefers the two large winter *Eudendrium*, which are its constant hosts.

24) *Amphinema dinema* (PÉRON & LESUEUR)

Depth-range: 0.5–20 m
 Occurrence: always present; scarce.
 Substratum: algae, sponges, barnacles.

25) *Amphinema rugosum* (MAYER)

Depth-range: 0–20 m
 Occurrence: always present; frequent, sometimes abundant, especially in winter.
 Substratum: algae, sponges, hydroids, bryozoans, polychaete tubes.

Reproductive period: July–August.

Remarks: common on the big winter *Eudendrium*. This is the first record of the species from the Mediterranean.

**26) *Eudendrium armatum*
TICHOMIROFF**

Depth-range: 10–20m

Occurrence: January, July; rare.

Substratum: concretions.

Reproductive period: July.

Remarks: only occasionally present in the study area, while very abundant in small caves and crevices and, at a deeper level (50 m), on rocks and ship wrecks. The stout outline of the species is very similar to that of *E. rameum* (PALLAS) which, in spite of extensive collections, has never been found in the studied area. *E. armatum* has been probably often recorded as *E. rameum*.

27) *Eudendrium capillare* ADLER

Depth-range: 0–5 m

Occurrence: always present; frequent, occasionally abundant.

Substratum: rock, concretions, algae, hydroids, bryozoans, mussels, barnacles.

Reproductive period: September–October.

28) *Eudendrium glomeratum* PICARD

Depth-range: 6–20 m

Occurrence: October–April; very abundant.

Substratum: concretions.

Reproductive period: October–March.

Remarks: stems deprived of polyps or with degenerating polyps have occasionally also been found from April to September. *Eudendrium glomeratum* is abundant below 10m. Its large colonies, together with those of *E. rumosum*, form a well defined winter facies. A very abundant fauna is associated with *E. glomeratum*. The study of the dynamics of its population and its biology will be the subject of separate papers.

**29) *Eudendrium fragile*
MOTZ-KOSSOWSKA**

Depth-range: 10–20m

Occurrence: September–May; frequent and abundant.

Substratum: algae, hydroids, bryozoans.

Reproductive period: October–March.

Remarks: According to PICARD's unpublished data (BOULLON, pers. comm.), in the Mediterranean there are three *Eudendrium* with macrobasal eurytele nematocysts, namely: *Eudendrium fragile*, *E. glomeratum*, *E. motzkossowskiae*. *Eudendrium glomeratum* has these nematocysts on the hydranth body, while *E. fragile* and *E. motzkossowskiae* have them both on the hypostome and the hydranth body. The distinction between the two species, according to PICARD, consists in the disposition of the tube within the capsule: it is spiraled along the main axis of the capsule in *E. motzkossowskiae*, along the secondary axis of the capsule in *E. fragile*. *Eudendrium motzkossowskiae*, furthermore, has hermaphroditic gonophores; along the Italian coast this species has been found associated with *Posidonia* leaves (BOERO, 1981b), as *E. fragile* can live on a variety of substrata. BOERO (1981b) did not distinguish the two species, but discussed the possibility that the Mediterranean *Eudendrium* with macrobasal euryteles on the hypostome and the hydranth body could be ascribed to two different forms, owing to the differences in reproduction and ecology.

**30) *Eudendrium racemosum*
(GMELIN)**

Depth-range: 0.5–20m

Occurrence: May–December; frequent and abundant.

Substratum: rock, concretions, algae, hydroids, gorgonaceans, barnacles, etc.

Reproductive period: June–October.

Remarks: *Eudendrium racemosum* reaches dimensions similar to those of *E. glomeratum*; it is very frequent and, at certain localities, abundant from 0.5 to 2–3 m. It never forms a facies because algae are superior competitors for space. *E. racemosum* is a typical superficial species, which reaches deeper levels by 'climbing' on other organisms (very often gorgonaceans) and shows a sharp tendency to "akrophily" (BOERO, 1984).

31) *Eudendrium ramosum* (L.)

Depth-range: 1–20m

Occurrence: always present (except June); very frequent and often very abundant.

Substratum: rock, concretions, algae, hydroids, barnacles.

Reproductive period: July–February.

Remarks: more abundant from October to March. Unlike *E. glomeratum*, it also lives in

shallow water, showing a wider ecological valence. It is very similar to *E. glomeratum*, and before PICARD (1951b) distinguished the two species they were probably confused. As is typical for hydroids living at both superficial and deeper levels, *E. ramosum* is small and stout in the first meters and more slender below 5–6m.

32) *Aequorea aequorea* (FORSKÅL)

Depth-range: 10–20m
Occurrence: November; rare.
Substratum: concretions, in small cracks.
Remarks: found only in the sampling from standard surfaces.

33) *Lafoeina tenuis* G. O. SARS

Depth-range: 0–20m
Occurrence: September–November; scarce.
Substratum: algae, *Posidonia* leaves, mussels.
Remarks: as all the other forms with campanulinid polyps, it is always rare, but this is often due to its small size, which makes its finding difficult during sorting operations.

34) *Laodicea undulata* (FORBES & GOODSIR)

Depth-range: 10–20m
Occurrence: November; rare.
Substratum: concretions, in small cracks.
Remarks: found only in the samples from standard surfaces.

35) *Mitrocoma annae* HAECKEL

Depth-range: 3–20 m
Occurrence: September–February; frequent, but always scarce.
Substratum: algae, hydroids.
Reproductive period: February.

36) *Campalecium medusifera*? TORREY

Depth-range: 3–20m
Occurrence: always present; frequent, but never abundant.
Substratum: algae, hydroids, barnacles.
Reproductive period: August–November.
Remarks: a short discussion of the species is given by BOERO (1981b).

37) *Halecium beanii* (JOHNSTON)

Depth-range: 0.5–20 m
Occurrence: April–December; not frequent, occasionally abundant.
Substratum: rock, concretions, algae, hydroids, barnacles.
Reproductive period: June, November, December.

38) *Halecium conicum* STECHOW

Depth-range: 5–15 m
Occurrence: September–January; scarce.
Substratum: algae, hydroids, bryozoans.

39) *Halecium halecinum* (L.)

Depth-range: 0.5–20 m
Occurrence: October–June; not frequent, occasionally abundant.
Substratum: concretions, algae, hydroids.
Reproductive period: October–December; some specimens fertile in June.

40) *Halecium labrosum* ALDER

Depth-range: 0.5–20 m
Occurrence: September–November; abundant.
Substratum: hydroids, bryozoans, barnacles.
Reproductive period: September–November.
Remarks: attains a considerable dimension (about 15 cm) and, in the limited period when present, it is abundant.

41) *Halecium lanckesteri*? (BOURNE)

Depth-range: 3 m
Occurrence: December; rare.
Substratum: barnacles.
Remarks: only one sterile colony has been found. Classification is doubtful.

42) *Halecium mediterraneum* WEISSMANN

Depth-range: 0.5–20 m
Occurrence: July–March; frequent and abundant.
Substratum: algae, sponges, hydroids, gorgonaceans, bryozoans, barnacles, mussels.
Reproductive period: July–November.
Remarks: the most frequent *Halecium* at Portofino, where, with the exception of the three spring months, it is an important component of the hydroid fauna. It is never a dominant

species, but its constant presence makes of it an element of primary importance in the species composition of the hydroid population.

43) *Halecium nanum* ALDER

Depth-range: 0.5–20 m
Occurrence: April–December; frequent, never abundant.
Substratum: algae.

44) *Halecium pusillum* SARS

Depth-range: 0–20 m
Occurrence: always present; very frequent, occasionally abundant.
Substratum: concretions, algae, *Posidonia*, hydroids, bryozoans, mussels.
Reproductive period: April, October.
Remarks: one of the more common species between 0 and 10 m. It reproduces asexually by means of planktonic propagula produced in October and November.

45) *Halecium tenellum* HINCKS

Depth-range: 0.5–20 m
Occurrence: October–March, July; scarce.
Substratum: algae, hydroids, bryozoans.

46) *Hydranthea margarica* (HINCKS)

Depth-range: 20 m
Occurrence: August; scarce.
Substratum: bryozoans (*Chartella tenella*).
Reproductive period: August.

47) *Ophiodissa mirabilis* (HINCKS)

Depth-range: 0.5–5 m
Occurrence: April, June, November; scarce.
Substratum: algae, barnacles.

48) *Filellum sepens* (HASSALL)

Depth-range: 0.5–20 m
Occurrence: August–April; frequent and abundant.
Substratum: hydroids, bryozoans, but mainly algae.
Reproductive period: February.

49) *Hebella brochi* (HADZI)

Depth-range: 3 m
Occurrence: November–March; not frequent, but abundant.
Substratum: *Synthecium evansi*.
Remarks: a strict epizoite of the hydroid *S. evansi*.

50) *Hebella parasitica* (CIAMICIAN)

Depth-range: 0–2 m
Occurrence: always present; frequent and abundant.
Substratum: hydroids.
Reproductive period: June–September.
Remarks: the systematics and ecology of the species in this area have been studied by BOERO (1980).

51) *Lictorella* ? sp.

Depth-range: 10–15 m
Occurrence: January–March; rare.
Substratum: algae.
Remarks: this is the first Mediterranean record of the genus. The lack of fertile material makes a certain classification impossible.

52) *Scandia gigas* (PIEPER)

Depth-range: 0.5–20 m
Occurrence: July–April; frequent and often abundant.
Substratum: concretions, algae, sponges, hydroids, bryozoans.
Reproductive period: August–September.
Remarks: the colonies can be stolonial or with branched stems, depending on different water movement conditions.

53) *Campanularia everta* (CLARKE)

Depth-range: 0–20 m
Occurrence: April–September; rare.
Substratum: algae and mussels.

54) *Campanularia hincksii* (ALDER)

Depth-range: 0.5–20 m
Occurrence: always present; frequent and often abundant.
Substratum: algae, sponges, hydroids, bryozoans, barnacles, ascidians.
Reproductive period: October–January.
Remarks: more abundant from September to April.

55) *Campanularia integra*

MACGILLIVRAY

Depth-range: 0–0.5 m

Occurrence: March–November; very frequent, occasionally abundant.

Substratum: algae, hydroids, barnacles, mussels.

Reproductive period: May–September.

Remarks: isolated colonies present down to 20 m depth.

56) *Clytia hemisphaerica* (L.)

Depth-range: 0–20 m

Occurrence: always present; very frequent, often abundant.

Substratum: concretions, algae, sponges, hydroids, bryozoans, mussels.

Reproductive period: August–March.

Remarks: one of the most common hydroid species in the world. Its great morphological variability is due to its great environmental tolerance.

57) *Clytia linearis* (THORNELY)

Depth-range: 1–20 m

Occurrence: always present; frequent, abundant in summer.

Substratum: algae, *Posidonia*, sponges, hydroids, bryozoans, polychaete tubes, etc.

Reproductive period: June, August, September, November.

Remarks: in summer the colonies reach considerable dimensions and liberate such a number of medusae as to cause small rashes to bathers.

58) *Clytia noliformis* (MCCRADY)

Depth-range: 0–10 m

Occurrence: April, August; rare.

Substratum: algae, mussels.

Reproductive period: August.

59) *Clytia paulensis* (VANHÖFFEN)

Depth-range: 5–20 m

Occurrence: September–April; frequent, never abundant.

Substratum: algae, hydroids, bryozoans.

Remarks: very frequent on *Eudendrium* in winter. In October propagula have been found.60) *Clytia* sp.

Depth-range: 3–6 m

Occurrence: October; rare.

Substratum: sponges of the genera *Petrosia* and *Ircinia*.

Remarks: It has also been collected in other

localities of the Ligurian Riviera and of the Gulf of Naples during the summer. Its hydrorhiza is always embedded in the bodies of

sponges. The ecology of this species, similar to that of *Sarsia halterata*, is very peculiar fora thecate hydrozoan. No other thecate form, in fact, is known to live in symbiosis with sponges. Kept in aquaria at 20°C for several months, *Clytia* sp. produced gonothecae containing a single medusa bud each. The produced medusae, totalling about fifteen, all developed in the same manner, reaching a development stage (in about ten days) with two radial canals and five mouths. None reached sexual maturity.61) *Laomedea calceolifera* (HINCKS)

Depth-range: 10–20 m

Occurrence: July–December; rare.

Substratum: algae, hydroids, gorgonaceans, bryozoans.

62) *Obelia bidentata* (CLARKE)

Depth-range: 20 m

Occurrence: May, September; rare.

Substratum: stones, concretions.

Reproductive period: May.

Remarks: reaches a considerable dimension (10 cm); as depth increases, it becomes more abundant.

63) *Obelia dichotoma* (L.)

Depth-range: 5–20 m

Occurrence: September–May; frequent, occasionally abundant.

Substratum: algae, gorgonaceans, bryozoans, ascidians.

Reproductive period: November–May.

64) *Obelia geniculata* (L.)

Depth-range: 0–2 m

Occurrence: always present; frequent.

Substratum: algae, mussels.

Reproductive period: January, March, May, July, October, November.

65) *Aglaophenia elongata*
MENEZHINI

Depth-range: 18–20 m
Occurrence: always present; frequent and abundant down to 50 m.
Substratum: rock, concretions, stones embedded in the mud.
Reproductive period: August.
Remarks: reaches a considerable size (20 cm) and is a constant component of the deeper levels at the studied site.

66) *Aglaophenia kirchenpaueri*
(HELLER)

Depth-range: 0.5–5 m
Occurrence: June–November, February, March; frequent, sometimes abundant in superficial crevices.
Substratum: concretions, sponges, barnacles.
Reproductive period: February, September, November.

67) *Aglaophenia octodonta* (HELLER)

Depth-range: 0–5 m
Occurrence: always present; frequent and abundant.
Substratum: rock, algae, sponges, barnacles, mussels.
Reproductive period: March–November.
Remarks: typically superficial, it characterizes the belt between 0 and 1 m.

68) *Aglaophenia picardi* SVOBODA

Depth-range: 0–20 m
Occurrence: August–March; frequent, never abundant.
Substratum: algae, sponges, barnacles.
Reproductive period: September–March.

69) *Aglaophenia tubiformis*
MARKTANNER-TURNERETSCHER

Depth-range: 0.5–15 m
Occurrence: September–May, frequent, never abundant.
Substratum: rock, concretions, algae, sponges, bryozoans, barnacles.
Reproductive period: February–May; September.

70) *Antennella secundaria* (GMELIN)

Depth-range: 7–20 m
Occurrence: always present; very frequent, never abundant.
Substratum: concretions, algae, hydroids.
Reproductive period: August–October.
Remarks: one of the most common species at Portofino; it often settles on the inferior part of the thallus of *Peyssonnelia* sp.

71) *Halopteris diaphana* (HELLER)

Depth-range: 5–10 m
Occurrence: June; rare.
Substratum: algae, concretions.
Reproductive period: June.
Remarks: scarce in the studied wall, in other localities of the Ligurian Riviera very common in the summer on rocky bottoms from 3 to 10–15 m, especially in well-illuminated sites.

72) *Kirchenpaueria echinulata*
(HINCKS)

Depth-range: 2–20 m
Occurrence: June–February; frequent, never abundant.
Substratum: algae, *Posidoni*, hydroids, barnacles.

73) *Nemertesia ventriculiformis*
(MARKTANNER-TURNERETSCHER)

Depth-range: 10 m
Occurrence: November; rare.
Substratum: algae.
Reproductive period: November.
Remarks: only one colony was found in the samples from standard surfaces.

74) *Plumularia obliqua* (JOHNSTON)

Depth-range: 0.5–20 m
Occurrence: February, September, October; abundant on *Posidoni*; rare on other substrata.
Substratum: *Posidoni*, hydroids, barnacles.
Reproductive period: October.

75) *Plumularia setacea* (L.)

Depth-range: 0.5–5 m
Occurrence: August, November; rare.
Substratum: hydroids, barnacles.

76) *Ventromma halecioides* (ALDER)

Depth-range: 0–15 m

Occurrence: June–September; scarce.

Substratum: algae, mussels, barnacles.

Remarks: in other localities of the Ligurian Riviera the species is fertile in summer.

77) *Synthecium evansi* (HELLER)

Depth-range: 2–3 m

Occurrence: October–March; rare, locally abundant.

Substratum: concretions, sponges.

Reproductive period: October, November.

Remarks: present, on the studied wall, in superficial crevices only; it is more common from 25–30 m depth. Since it can be present in superficial stations where water movement is intense and light is feeble, light should be the factor that regulates its distribution.

78) *Dynamena disticha* (Bosc)

Depth-range: 0.5–15 m

Occurrence: always present, except in April and May; frequent, abundant in summer.

Substratum: concretions, algae, hydroids, barnacles.

Reproductive period: July–November.

79) *Salacia desmoides* (TORREY)

Depth-range: 4–5 m

Occurrence: July; rare.

Substratum: algae.

Reproductive period: July.

80) *Sertularella crassicaulis* (HELLER)

Depth-range: 0.5–20 m

Occurrence: September–April; very frequent, never abundant.

Substratum: concretions, algae, hydroids, gorgonaceans, bryozoans.

Reproductive period: October–January.

Remarks: reaches a considerable size (10–20 cm) and its white colour is very evi-

dent. Near the surface it settles directly on concretions; as depth increases it tends to “climb” on erect organisms with the behaviour known as “akrophily” (BOERO, 1984). Below about 10 m it is almost always settled on *Eunicella cavolinii*, *Eudendrium glomeratum* and *E. ramosum*.

81) *Sertularella gaudichaudi* (LAMOUREUX)

Depth-range: 0–20 m

Occurrence: always present; frequent and abundant between 0 and 0.5 m; occasionally present at deeper levels.

Substratum: concretions, algae, hydroids, mussels, barnacles.

Reproductive period: February, April, August–December.

Remarks: PICARD (1956) has discussed the ecological forms of the present species under the name *S. ellisii*. CORNELIUS (1979) has synonymized *S. ellisii* with *S. gaudichaudi*, not retaining as valid all the forms listed by PICARD. Distinctions on the basis of PICARD's criteria are nevertheless possible in the present material. Near the surface the species is present with the form *lagenoides* while, as depth increases, the forms *ornata* and *mediterranea* are present. The *lagenoides* form is always present from 0 to 1–2 m and is a characteristic component of the superficial benthic population. The other forms have been found sporadically and in small quantities.

82) *Sertularella polyzonias* (L.)

Depth-range: 5–15 m

Occurrence: November, December; rare.

Substratum: algae.

Reproductive period: November.

83) *Sertularia perpusilla* STECHOW

Depth-range: 12 m

Occurrence: always present, locally abundant.

Substratum: *Posidonia* leaves.

Reproductive period: September.

Remarks: found only on a few *Posidonia* plants present on the studied wall at 12 m.

Other species found at Portofino and nearby zones

Samplings carried out in other zones and the examination of the literature on Ligurian hydroids have revealed the existence of other species on the Portofino Promontory and the surrounding coast, namely:

84) *Sarsia* sp.

Depth-range: 5 m

Occurrence: summer; rare.

Substratum: sponges.

Remarks: found in one of the sponges colonized by *Clytia* sp. Its particular behaviour does not allow discovery from preserved material. The polyps, in fact, can completely retract within the sponge if disturbed. Like *Clytia* sp. this is probably a new species.

85) *Paracoryne huvei* PICARD

Depth-range: 0-1 m

Occurrence: winter; frequent and locally abundant.

Substratum: rock, mussels.

Reproductive period: winter.

Remarks: BOUILLON (1975) has studied its ecology. BOERO (1981 a) has recorded this species outside the area of its discovery. It is very common along the Ligurian coast and has also been found in Sardinia.

**86) *Eudendrium motzkossowskiae*
PICARD**

Depth-range: 0-1 m

Occurrence: always present; frequent, never abundant.

Substratum: *Posidonia* leaves.

Reproductive period: summer.

Remarks: see *Eudendrium fragile* (29).**87) *Aglaophenia harpago*
VON SCHENK**

Depth-range: 2-30 m

Occurrence: always present; frequent, locally abundant.

Substratum: *Posidonia* leaves.

Reproductive period: summer.

88) *Kirchenpaueria pinnata* (L.)

Depth-range: 50 m

Occurrence: not observed (collected in July).

Substratum: stones.

Reproductive period: July.

89) *Nemertesia antennina* (L.)

Depth-range: 40-50 m and deeper.

Occurrence: not observed (collected in July); frequent and abundant.

Substratum: mud, stones.

Remarks: below about 40 m it forms large meadows together with *Thecocarpus myriophyllum*.

90) *Thecocarpus myriophyllum* (L.)

Depth-range: 40-50 m and deeper.

Occurrence: not observed (collected in July); frequent and abundant.

Substratum: mud.

Seven other species have been reported by ROSSI (1949-50; 1961) from the Portofino Promontory and nearby zones, namely: *Halocordyle disticha* GOLDFUSS, *Halecium petrosus* STECHOW, *Acryptolaria conferta* (ALLMAN), *Hebella scandens* BALE, *Antennella siliquosa* HINCKS, *Halopteris liechtensterni* (MARK-TANNER-TURNERETSCHER).

The 97 species recorded to date from the Portofino Promontory and nearby zones are about the half of the total number of hydroid species in the Mediterranean.

The high number of species found in the present study is not surprising. The species richness of Portofino is probably a general feature of the hydroid populations of Mediterranean hard bottom communities. The imperfect knowledge of the ecology and distribution of hydroids in the Mediterranean probably has historical roots. Especially in the last century, but even today, field observation and collection were limited to the "good season": the summer. Very

often, teaching duties and bad weather conditions prevented a continuous presence of researchers in the field. The result is an incomplete knowledge of hydroid populations which, on the other hand, are particularly rich in winter. In the last decades new species, genera, and families usually absent in summer have been discovered, among them *Paracoryne huvei*, *Rhysia autumnalis*, *Eudendrium glomeratum*.

Summary

The hydroid community of Portofino is extremely rich in species. These are vertically zoned so as to form two distinct cenotic units separated by a sharp discontinuity (superficial discontinuity). This separation persists in time. The upper unit is composed of a set of species that are adapted to high levels of environmental energy. It shows a remarkable stability in time. The deeper community shows a greater degree of variation in time: two distinct aspects appear, in the warm and in the cold season respectively. Fertility was found to be rather constant in the superficial community and variable with season in the deep one. The above zonation is the response to a complex gradient of light and water movement. Temperature seems to play a minor role. In the upper faunal zone water movement intensity and type seem to be the selecting factor. As for light intensity, the response of the community is less clear. Beyond the superficial discontinuity, temperature and competition for the substratum influence the seasonality of the community. A comparison of the present results with the commonly accepted bionomic models of the Mediterranean benthos reveals that the observed superficial discontinuity of the hydroid population is identical with RIEDL's first critical depth. RIEDL's second critical depth is not identifiable. In the light of these results, the infralittoral zone defined by PÉRÈS and PICARD is far from being homogeneous and must be split in two distinct zones.

References

- BENZECRI, J. *et al.*, 1973: L'analyse des données. Vol. II. L'analyse des correspondences. Dunod, Paris; 615pp.
- BOERO, F., 1980: *Hebella parasitica* (Cnidaria, Hydroida): a thecate polyp producing an anthomedusa. *Mar. Biol.*, **59** (3): 133–136.
- , 1981a: Osservazioni ecologiche sugli idroidi della fascia a mitili della Riviera Ligure di Levante. *Cah. Biol. Mar.*, **12**: 107–117.
- , 1981b: Systematics and ecology of the hydroid population of two *Posidonia oceanica* meadows. *P. S. Z. N. I: Marine Ecology*, **2** (3): 181–197.
- , 1984: The ecology of marine hydroids and effects of environmental factors: a review. *P. S. Z. N. I: Marine Ecology*, **5** (2): 93–118.
- , L. CHESSA, C. CHIMENZ & E. FRESI, 1985: The Zonation of Epiphytic Hydroids on the Leaves of Some *Posidonia oceanica* (L.) DELILE Beds in the Central Mediterranean. *P. S. Z. N. I: Marine Ecology*, **6** (1): 27–33.
- BOUDOURESQUE, C. F. & F. CINELLI, 1977: Le peuplement algal des biotopes sciaphies superficiels de mode battu en Méditerranée Occidentale. *Pubbl. Stn. Zool. Napoli*, **40** (2): 433–459.
- BOUILLON, J., 1975: Sur la reproduction et l'écologie de *Paracoryne huvei*, PICARD (*Tubularoidea - Athecata - Hydrozoa - Cnidaria*). *Arch. Biol.*, **86** (1): 45–96.

- BRINCKMANN-VOSS, A., 1970: *Anthomedusae/Athecatae (Hydrozoa, Cnidaria)* of the Mediterranean. Part I: *Capitata*. Fauna e Flora del Golfo di Napoli, **39**: 1-96.
- BROCK, M. A., 1975: Circannual rhythms - 111. Rhythmicity in the longevity of the hydranth of the marine cnidarian *Campanularia flexuosa*. Comp. Biochem. Physiol., **51** A: 391-398.
- CÉHSSAT, R., 1976: Exercices commentés de statistique et informatique appliquées. Dunod, Paris; 232 pp.
- CINELLI, F., E. FRESI, L. MAZZELLA, M. PANSINI, R. PRONZATO & A. SVOBODA, 1976: Distribution of benthic phyto- and zoocoenoses along a light gradient in a superficial marine cave. In: B. F. KEEGAN, P. O. CEIDIGH & P. J. BOADEN (Eds.), Biology of benthic organisms. Pergamon Press, Oxford and New York: 173-183.
- CORNELIUS, P., 1979: A revision of the species of *Sertulariidae (Coelenterata: Hydroida)* recorded from Britain and nearby seas. Bull. Br. Mus. (Nat. Hist.) Zool., **34** (6): 243-321.
- DELLA CROCE, N., M. FABIANO & T. ZUNINI SERTORIO, 1979: Biomassa planctonica, sali nutritivi, parametri idrologici. (Chiavari): Ottobre 1977-Ottobre 1978. Università di Genova, Cattedra di Idrobiologia e Piscicoltura. Rapporto tecnico N. 8: 1-14.
- , M. FABIANO & T. ZUNINI SERTORIO, 1980: Biomassa planctonica, sali nutritivi, parametri idrologici. (Chiavari): Ottobre 1978-Ottobre 1979. Università di Genova, Cattedra di Idrobiologia e Piscicoltura. Rapporto tecnico N. 11: 1-14.
- FRESI, E., C. CHIMENZ & G. MARCHIO, 1982: Zonazione di Briozoi ed Idroidi in una prateria di *Posidonia oceanica* (L.) DELILE. Naturalista Sicil., S. IV, 6 (Suppl.), **3**: 499-508.
- & F. CINELLI, 1982: La discontinuità superficiale: appunti per una nuova interpretazione del benthos mediterraneo. Boll. dei Mus. Ist. Biol. Univ. Genova, **50** (Suppl.): 194.
- & C. GAMBI, 1982: Alcuni aspetti importanti dell'analisi matematica di ecosistemi marini. Naturalista Sicil., S. IV, 6 (Suppl.), **3**: 449-465.
- FRONTIER, S., 1974: Contribution à la connaissance d'un écosystème néritique tropical: étude descriptive et statistique du peuplement zooplanctonique de la région de Nosy-Bé (Madagascar). Thèse Doct. Univ. Aix-Marseille; 628 pp.
- HATHEWAY, W., 1971: Contingency-table analysis of rain forest vegetation. In: G. B. PATIL, E. C. PILOU & X. WATERS (Eds.), Statistical ecology. Pennsylvania State University Press, **3**: 271-307.
- HILL, M., 1973: Reciprocal averaging: an eigen-vector method of ordination. J. Ecol., **61**: 237-249.
- JANCEY, R., 1974: Algorithms for detection of discontinuities in data sets. Vegetatio, **29**: 131-133.
- MARINOPULOS, J., 1983: Essai d'interprétation de la répartition des espèces benthiques des substrats durs à partir d'enregistrements de variations de l'éclairement. Rapp. Comm. Int. Mer Médit., **28** (3): 211-212.
- MERGNER, H., 1977: Hydroids as indicator species for ecological parameters in Caribbean and Red Sea coral reefs. In: D. L. TAYLOR (Ed.), Proceedings, Third Int. Coral Reef Symp.; Univ. Miami, Florida, **1**: 119-125.
- MOORE, J., 1939: The role of temperature in hydranth formation in *Tubularia*. Biol. Bull., **76** (1): 104-107.
- MUUS, B., 1968: A field method for measuring "exposure" by means of plaster balls. Sarsia, **34**: 61-68.
- NEPPI, V., 1917: Osservazioni sui polipi idroidi del Golfo di Napoli. Pubbl. Stn. Zool. Napoli, **2**: 29-65.
- ORLOCI, L., 1975: Multivariate analysis in vegetation research. Dr. W. Junk B. V. Publ., The Hague; 276 pp.
- PÉRÈS, J. & J. PICARD, 1964: Nouveau manuel de bionomie benthique de la Mer Méditerranée. Recl Trav. Stn Mar. Endoume, **31** (47): 1-137.
- PICARD, J., 1951a: Les hydraires des formations coralligènes des côtes Françaises de la Méditerranée. Vie Milieu, **2** (2): 254-261.
- , 1951b: Note sur les hydraires littoraux de Banyuls-sur-mer. Vie Milieu, **2** (3): 338-349.
- , 1952: Les hydrozoaires des herbiers de Zostéracées des côtes Françaises de la Méditerranée. Vie Milieu, **2** (Suppl.): 217-233.
- , 1956: Les espèces et formes Méditerranéennes du genre *Sertularella*. Vie Milieu, **7** (2): 258-266.
- RIEDEL, R., 1959: Die Hydroiden des Golfes von Neapel und ihr Anteil an der Fauna unterseeischer Höhlen. Ergebnisse der Österreichischen Tyrrhenia-Expedition 1952. Teil 16. Pubbl. Stn. Zool. Napoli, **30** (Suppl.): 589-755.

- , 1964: 100 Jahre Litoralgliederung seit Josef Lorenz, neue und vergessene Gesichtspunkte. *Int. Rev. ges. Hydrobiol.*, **49**: 281-305.
- , 1971: Water movement. 5.3. Animals. In: O. KINNE (Ed.), *Marine Ecology*. Wiley Interscience, London: 1123-1156.
- ROSSI, L., 1949-50: Celenterati del Golfo di Rapallo. *Boll. Mus. Zool. Univ. Torino*, **20**: 194-235.
- , 1961: Idroidi viventi sulle scogliere del Promontorio di Portofino (Golfo di Genova). *Ann. Mus. Civ. Stor. Nat. Genova*, **72**: 69-85.
- SARÀ, M., A. BALDUZZI, F. BOERO, M. PANSINI, D. PESSANI & R. PRONZATO, 1978: Analisi di un popolamento bentonico di falesia del Promontorio di Portofino: dati preliminari. *Boll. dei Mus. Ist. Biol. Univ. Genova*, **46**: 119-137.
- STECHOW, E., 1919: Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete. *Zool. Jahrb. Abt. Syst.*, **42**: 1-172.
- , 1923: Zur Kenntnis der Hydroidenfauna des Mittelmeeres, Amerikas und anderer Gebiete, 11. *Zool. Jahrb. Abt. Syst.*, **47**: 29-270.
- SVOBODA, A., 1979: Beitrag zur Ökologie, Biometrie und Systematik der mediterranen *Aglao-phenia*-Arten (Hydroidea). *Zool. Verh. Rijksmus. Nat. Hist. Leiden*, **167**: 3-114.